THE FORM AND STRUCTURE OF *CTENOZAMITES CYCADEA* (BERGER) SCHENK

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Pp. 159–173 ; *Plates* 31, 32 ; 2 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 5 No. 6
LONDON : 1961

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series, corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

This paper is Vol. 5, *No.* 6 *of the Geological (Palaeontological) series.*

PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

Issued July, 1961 *Price Seven Shillings and Sixpence*

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By T. M. HARRIS

SYNOPSIS

This paper deals with a single magnificent specimen of the Lower Liassic leaf which has been called *Ctenopteris cycadea* (Brongn.). It is nearly complete and shows that the leaf is larger than had been supposed and also proves that the rachis forks. This forking brings *Ctenozamites* close to *Ptilozamites* and possibly also to *Odontopteris*. The specimen has also the merit of being partially petrified and gives some indication about its internal tissues.

INTRODUCTION

The specimen (V.36330) bears the label " Plant from the Flatstones Nodules, Black Marl, Black Ven, Charmouth, Dorset. Collected by J. F. Jackson, 27-9-58." The rock is from the Flatstones of bed 83 of the Lower Lias succession of Dorset (Lang & Spath, 1926), and contains the well-known ammonites *Asteroceras obtusum* (J. Sowerby) and *Promicroceras planicostata* (J. Sowerby) which fix its age as the Obtusum Subzone, the lowest division of the Obtusum Zone. The specimen was in a large concretion which fell from the cliff and when the boulder was split it was shattered. Most of the pieces were reassembled, including some of the Counterpart, which, together with the Part, was used in the drawing in Text-fig. 1.

The flora of the British Lower Liassic is small and the floras of the Middle and Upper Liassic are even smaller. Land plants occur in its extremely limited fresh-water facies (see Kendall, 1949 for West Scotland, Lewarne & Pallot, 1957 and Harris, 1957 for South Wales). In its widespread marine facies, plants, apart from driftwood, seem to be very rare, but a moderate number have been collected over the last century and most of these are magnificent specimens. The flora was described by Seward in 1904 and since then some additional species have been collected and others have been revised.

The flora is as follows (the list may include some from the Rhaetic) :

" *Carpolithes* sp." Seward, 1904.

" ? *Araucarites* sp." Seward, 1904, p. 20.

Cycadolepis sp. (as *Hippurites* Buckman and indeterminable according to Seward, 1904).

Equisetites sp. (as *E. muensteri* Seward, 1904).

Cycadopteris anglica Gothan = *Thinnfeldia rhomboidalis* of Seward, under revision by Townrow & Hancock.

Ctenozamites cycadea (Berger) of this paper = *Ctenopteris cycadea* of Seward.

The previously known specimens are in a soft shale from Lyme Regis.

Cycadites rectangularis Brauns, see Seward, 1904.
Otozamites bechei Brongn. (as *O. obtusus* L. & H. in Seward, 1904 ; see also Harris, 1960).
Cycadeoidea (*Yatesia*) *gracilis*, Seward, 1904. (A *Bucklandia*.)
Cycadeoida pygmaea L. & H. (specimen not seen, see Seward, 1904).
Pagiophyllum peregrinum. See Seward, 1904, Kendall, 1948.
Strobilites elongata L. & H. (specimen not seen ; see Seward, 1904).
Pagiophyllum sewardi Kendall, 1948.

In addition there are in the British Museum a leaf resembling *Stenopteris*, a forked leaf or branch with parallel veined pinnae (or leaves) and some alga-like filaments. In the Geological Survey Museum there are also :

" *Zamites megaphyllos* Phillips " (a large, simple leaf).
" *Cupressinites liasinus* " (possibly distinct from *Pagiophyllum peregrinum*).

Several of these fossils, and also the fossil wood, might yield information beyond what has been published.

The specimens come from numerous quarries and coastal exposures in the SW. of England and by far the richest region is around Lyme Regis, Dorset, which has provided more than half the specimens. Unfortunately the specimens, apart from those collected by Mr. Jackson, are imperfectly localized being merely labelled " Lyme Regis ". Most of them are in a soft black shale, presumably exposed between the tide marks, but the exact locality is lost to memory and the specimens could be from one or more zones. I spent a few days searching at Lyme Regis and merely found a good deal of drift wood, some of it with structure preserved but no leaf or twig. There were no cuticle fragments in the blocks I macerated.

DESCRIPTION

Form. The two pieces fitted together are 55 cm. long, but the apex is lost and so is the base of the rachis. It is possible to estimate the length of the missing top from the taper of the half rachises, which is about 1 mm. in 5 cm. As the width at the top is 7 mm. the missing part might be 35 cm. long, but rather less if the rachis tapered more quickly in the upper and more leafy part and this would seem likely. The petiole increases in width downwards and is about 2 cm. wide at the point where the rock is broken. There is nothing to suggest how much of the original leaf is missing. Thus the leaf, apart from the missing base, may have been 80 or 90 cm. long. The lower pinnae are severely abraded and some must have disappeared altogether, but those between the forks of the rachis which may have been protected are better preserved. The most complete is 11 cm. long, but the pinnae below the fork have distinctly larger pinnules and were perhaps rather longer. It will be noticed that the pinnae of the right fork are alternate and those of the left nearly opposite. The lowest basiscopic pinnules are borne just below the point of attachment of the pinna, that is, on the main rachis, but the plane of cleavage has not followed the specimen perfectly and only a few are seen. These first pinnules arise on the upper surface of the rachis and the later pinnules arise near the top of

FIG. 1. A, silhouette of the whole specimen, V.36330. There is a gap between the top 4 cm. and the rest. The top is drawn from part and counterpart. Reduced to 1/3 natural size. B, tissues of vascular bundle of rachis in horizontal section, some bundle sheath cells enclose one or two scalariform tracheids, V.36330*a*. × 200. C, surface of rachis in horizontal section, showing from the top downwards: cuticle, epidermal cell contents, stone cells flanked by narrow cells, V.36330*a*. × 200.

the pinna rachis. The pinnules are almost flat but with slightly depressed margins and in none is the margin rolled back. The pinnules have obtuse apices, in none was it mucronate or denticulate. Their veins are clearly seen where the plane of cleavage has passed through them. They diverge slightly and some fork ; maintaining a concentration of about 20 per cm.

Anatomy of lamina. The fossil is preserved in an unusual way, intermediate between a compression and a petrefaction. The lamina is only slightly compressed and when buried in the marine calcareous mud seems to have undergone two changes. The first is that most of the cells became filled with a brown or black bituminous substance (there seems too much of it to represent the original cell contents), and second that the spaces between the cells were filled with calcite. The fossil as exposed is a light brown colour when dry. The lamina cannot be picked off the rock, a hard limestone, but chips can be treated with dilute acid when pieces of the lamina, especially its epidermis are freed. They were studied in three ways:

1. The cuticles were prepared.
2. The internal tissues were teased apart after decalcification.
3. The internal tissues were studied in sections.

The cuticles were rather difficult to prepare because nitric acid attacks the substance of the cuticle almost as rapidly as the mesophyll cells. Good results were obtained as follows :

1. The decalcified epidermis was soaked in moderately strong nitric acid for 10–60 min.

2. It was washed in dilute ammonia.

3. It was left in glycerine on a slide for several hours. This seems to toughen it.

4. The mesophyll cells were carefully teased away from its inner side. Even after this treatment the cell contents remain and the preparation is of the epidermis rather than purely of the cuticle.

The isolation of internal tissues by teasing was only moderately successful. The palisade mesophyll cells are very conspicuous as little dark cylinders representing their contents ; their walls are not seen in teased preparations.

The upper cuticle is thick and shows the outlines of polygonal epidermal cells. These cells are almost uniform, the veins being scarcely distinguishable. The outlines of the cells are marked by broad but by no means prominent ridges. The sides of the cells are straight but interrupted by a few pits. The surface walls are flat and the surface may be finely granular or the granules may be elongated and this appearance seems to pass gradually into a system of fine parallel striations orientated longitudinally. Only one trichome base was seen on the upper side (Text-fig. 2F) ; it is like those along the veins on the lower side and consists of a small rounded cell on top of the ordinary epidermal cells.

The lower cuticle is also thick. The cells are like those of the upper side, but smaller and the veins are clearly shown by about five rows of elongated rectangular cells and no stomata ; the wide intervenal areas have irregular or isodiametric cells and numerous scattered stomata. The guard cells are mostly longitudinally orientated or more or less oblique, but seldom transverse. They are at the bottom

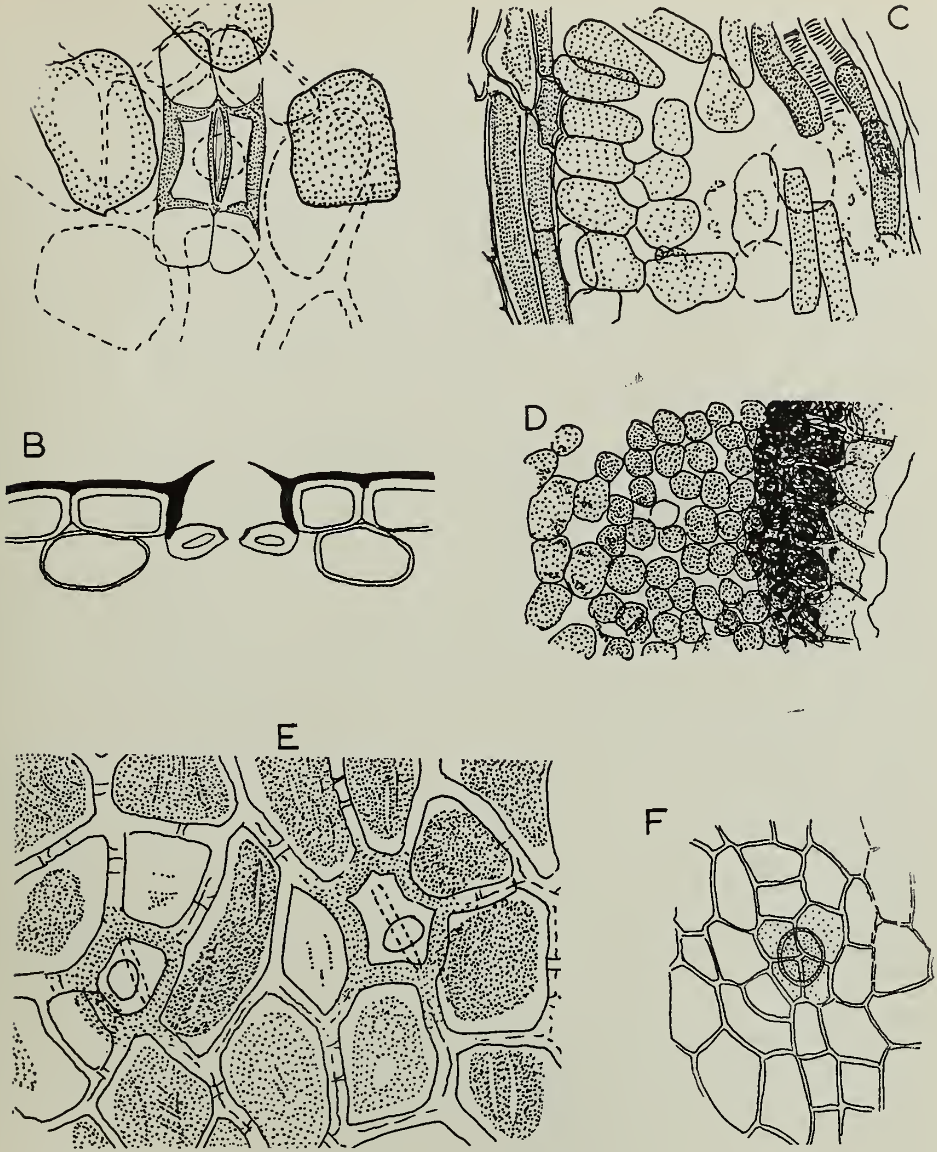

FIG. 2. *Tissues of lamina*

A, a stoma seen from within. A few mesophyll cells remain ; the epidermis at a deeper level of focus is shown by broken lines, V.36330*b*. × 800. B, imaginary T.S. through A, the vertical distances being determined by focusing. Cuticle in black, other walls outlined, × 800. C, horizontal section through middle of mesophyll showing a vein with sheath and tracheids (right) and the sheath along (left), V.36330*c*. × 200. D, horizontal section through upper surface of lamina showing from right to left, cuticle, epidermal cell walls, epidermal cell contents, outer layer of palisade, deeper layer of palisade mesophyll, V.36330*d*. × 200. E, lower cuticle from outside. The content is still present in most epidermal cells. Faint surface striations are shown by dotted lines and the guard cell aperture at a deeper focus by a pair of broken lines, V.36330*b*. × 800. F, upper cuticle showing a complex trichome base, V.36330*e*. × 200.

of a polygonal or rectangular pit with a thickly cutinized wall formed by an irregular ring of about six subsidiary cells. The mouth of the pit is covered by a strongly raised dome (almost a hemisphere) of thin cuticle. The top of this dome is pierced by a hole which may be round or oval and is often more or less transversely elongated. Encircling cells may occur but are inconstant.

The guard cell surface is thinly cutinized but there is a slightly thickened band by the aperture. The aperture itself is arched, the middle part being more deeply sunken than the ends. The outline of the poles of the guard cells can just be traced, but nothing remains of any lignine thickenings originally present in the guard cells.

The epidermis is scarcely compressed and it was possible to recognize differences of level of the stomata by focusing. The top of the dome is about 8 μ above the general surface of the cuticle and the middle part of the stomatal aperture is about 8 μ below this surface.

Trichome bases are frequent on the veins and consist of one or occasionally two small oval cells on top of the ordinary cells. Sometimes a ring is visible on the surface of one of these cells but more often the whole cell surface would seem to have been covered by the trichome. No hypodermal cells occur, but fibres along the veins come close to the upper epidermis.

The mesophyll was studied successfully both by maceration and horizontal sections. The palisade mesophyll is well developed and consists of at least two, probably more, layers of closely packed cylindrical cells 20 μ wide and 50 μ long. In the middle region of the lamina, at the sides of the veins, the mesophyll cells are oval and orientated transversely. Their walls appear to be thin. In the lower part of the leaf the mesophyll cells are of irregular shapes, but next the lower epidermis they are oval again. There is a gap above each stoma and the mesophyll cells here tend to be rather elongated, about five forming a ring. The veins were seen in sections. They have a sheath of elongated cells with massive dark contents. These cells appear to have transverse ends, but it is difficult to distinguish between a transverse break and a true end. The walls as far as they were seen are only moderately thick and not obviously pitted. This sheath is in contact with the spongy mesophyll and encloses various narrow elongated cells, which have little or no bituminous filling but are merely preserved as poorly seen walls. Most of these elongated cells are narrow and show no obvious features, they presumably are fibres and perhaps sieve tubes. In addition a few small tracheids were seen. They have scalariform thickening.

The leaf contains no resin cavities in the mesophyll. There is no sign of any secretory duct in the veins, but unless such a duct had obvious contents it might be hard to recognize in horizontal section.

Anatomy of rachis. The rachises are preserved in the same way as the lamina, but underwent far more compression before they were calcified. Thus the main rachis or petiole which is 2 cm. wide is barely 1 mm. thick in the fossil. Most of its substance has been lost, but a few small chips were obtained when pieces covered by the matrix were exposed. As with the lamina, the plane of cleavage passes through the rachis substance rather than outside it, so each fragment has one epidermis and more or less of the internal tissues. The broken surface showed elongated cells but nothing else clearly.

Good pieces of cutinized epidermis together with isolated cells from the interior were obtained by soaking chips in dilute acid. These represent the various thick-walled tissues seen in the sections, apart from the tracheids which did not survive this treatment. Sections were again cut in a nearly horizontal plane but efforts to obtain more transverse ones gave no useful result.

The epidermis is probably more thickly cutinized than that of the lamina and it was easy to obtain a good preparation, though the dark contents of the epidermal cells usually remains. The cells are elongated and have straight, conspicuous walls and the surface is longitudinally striated. No trichomes were seen but stomata are rather frequent and well developed. The subsidiary cell group is elongated, the guard cells longitudinal and the pore in the dome is rather large and also longitudinally orientated. A well developed sclerotic layer occurs underneath the epidermis. This layer has at least three sorts of cells. The most conspicuous are thick-walled cells looking like elongated stone cells and with conspicuously pitted walls. Then there are strands of narrow fibre-like cells without much contents. Finally there are short thin-walled cells full of black contents which are regarded as assimilatory parenchyma. Some of these are just under a stoma where they are arranged in a ring to form a substomatal air cavity. In the cells like stone cells the dark content is slightly contracted and forms spikes which are evidently the filling of large pits. The cell wall is not very clearly seen but the pits show that it was thick. The ends of these cells may be more or less transverse, or they may be obtusely pointed. This sclerotic layer is by no means thick, in the slightly oblique section it appears about five times as broad as the epidermis so that it can be inferred that it is about five times as thick.

The tissue inside the sclerotic layer which must have formed most of the massive petiole shows several kinds of cells, but most of it is disorganized to a brown humus-like substance. It may well be that this substance was originally parenchyma but the outlines of its cells are not clearly seen. This contrasts with the lamina where the mesophyll cells were filled with dark bituminous matter and very clearly seen.

Most of the cells clearly preserved in the interior of the petiole are elongated ones with dark contents and just like those forming the bundle sheath in the lamina. In the horizontal section these cells form numerous longitudinal files and while some of them probably form bundle sheaths, they are so numerous that most are probably scattered through the tissues. Numerous small vascular bundles were recognized by the presence of scalariform tracheids (Text-fig. 2) but as in the lamina these tracheids were poorly preserved. No massive strands of tracheids occur. In a few bundles there are possibly tracheids transitional between scalariform and multiseriate pitted, that is to say they seem to have thick walls marked with longitudinal rows of small oval pits. The appearance was, however, obscure and it is possible that the cells concerned are of different nature. The bundles include other elongated cells but nothing could be learnt about the arrangement of the cells in these bundles.

DISCUSSION

1. *Determination.* This specimen, apart from being more complete than usual, agrees in every respect with typical leaves of *Ctenozamites cycadea* and with no other species. *C. cycadea* was already known from this locality and if only a small part from the top had been collected it would have been an ordinary specimen. Indeed if no more than one or two pinnules showing their venation had been available, as in Berger's holotype, it could still have been determined with confidence. The most similar fossils are other species of *Ctenozamites*, particularly the Oolitic *C. leckenbyi* where, however, the pinnules are usually longer and acuminate and *Ptilozamites nilssoni* of the Rhaetic (see Harris, 1932), where the leaf is simply pinnate but small fragments look similar.

The cuticle of the present specimen looks just like that of a French specimen figured by Mme. Corsin (1950). It also agrees with the upper cuticles (which alone could be prepared) of the English Liassic leaf, Brit. Mus. (N.H.) no. 40, 674, and with the specimen figured by Saporta (1873, pl. 40, fig. 2) of which Dr. Archangelsky showed me a preparation. The cuticle thus fully confirms the identification.

To judge from its pinnules the present specimen was a leaf of average size. Fragments with smaller pinnules have been figured as for example by Schenk (1887) and these might belong to smaller leaves but there are also fragments with distinctly larger pinnules, as for example, Brit. Mus. (N.H.) no. 40, 674, figured by Seward (1904, pl. 3, fig. 1). The detached pinnule which Mme. Corsin (1950) determined as *Ctenopteris* cf. *sarrani* may be an unusually large form of *Ctenozamites cycadea* (with which it is associated) and if so may represent a leaf twice as large as the present specimen.

2. *Habitat and age.* The present specimen and the two others known from England were found near Lyme Regis, Dorset, in marine Lower Lias. The limestone there is well provided with ammonites, but it also contains very occasional leaves and pieces of wood of land plants. The French specimens figured by Saporta (1873) seem to have a similar origin and so apparently do the German ones of Germar (1847) and Salfeld (1912). This occurrence in marine rocks may be significant even though it also occurs in rocks of fresh water origin (Corsin, 1950). It would be interesting to know more about the provenance of the numerous other specimens described.

If this species does prove exceptionally common in marine rocks, it would suggest that the plant grew near the sea, perhaps near the strand of a tidal river, where it would have a special chance of being preserved at the sea bottom. The same may be true of *Otozamites bechei* (*O. obtusus*).

The present specimen is well dated, being in a matrix full of ammonites, and many others are in rocks zoned by ammonites as Lower Liassic age, as in several parts of Germany (see Salfeld, 1907, 1909). It also occurs in localities regarded as Rhaetic, but some of these belong to the " Grenzschichten " which were formerly regarded as Rhaetic, but shown by Gothan (1914) to be Lower Liassic.

The age of others may be unsettled, but I am not aware of any specimen of *C. cycadea* which occurs in beds with the Rhaetic *Pteria contorta*. The question is worth investigation because this should be a valuable zone fossil.

Specimens agreeing with *C. cycadea* have been found in the Lower Oolite of Roseberry Topping, Yorkshire. If these are correctly determined the species would extend through the Lias.

3. *Nomenclature.*

Select list of references to *Ctenozamites cycadea* :

1832 *Odontopteris cycadea* Berger, p. 23, pl. 3, figs. 2, 3.
1836 *Filicites cycadea* (Berger) Brongniart, p. 387, pl. 129, figs. 2, 3.
1873 *Ctenopteris cycadea* (Brongniart) Saporta, p. 355, pl. 40, figs. 2–5, pl. 41, fig. 1, 2.
1882 *Ctenopteris cycadea* (Brongn.) : Staub, p. 249 and plate.
1886 *Ctenozamites bergeri* (Goeppert) Nathorst, p. 122 (Name).
1887 *Ctenozamites cycadea* (Brongn.) Schenk, p. 5, pl. 3, fig. 11–16a, pl. 4, fig. 18 ; pl. 6, fig. 30 ; pl. 7, fig. 36 ; pl. 8, fig. 43 ; pl. 9, fig. 54. (Includes a forked specimen.)
1904 *Ctenopteris cycadea* (Brongn.) : Seward, p. 36, pl. 3 ; fig. 1, 1*a* ; probably text-fig. 2.
1950 *Ctenopteris cycadea* (Brongn.) : Corsin, p. 258, pl. 11, fig. 3 ; pl. 12, figs. 6–11, text-figs. 6, 8. (Perhaps large pinnules and cuticles described as *C.* cf. *sarrani* should also be included in *C. cycadea*.)

The name used for this leaf by most authors is *Ctenopteris cycadea* (Brongn.), but both generic name and authority are wrong. The first specimens described, and fortunately reasonably well figured, were those called *Odontopteris cycadea* by Berger (1832) from the Rhaetic (or Lower Lias) of SW. Germany. Some have suggested that " *Filicites agardhiana* " of Brongniart (1824) belonged to it but both Nathorst (1909) and Antevs (1919) who examined the Swedish specimen agree that it does not, but very probably is a bad specimen of *Dictyophyllum nilssoni*. Possibly the reason why the species has been attributed to Brongniart rather than to Berger is that the first part of Brongniart's Histoire appeared in 1828, and the fact that Liv. 10 with *Filicites cycadea* only appeared after Berger's work is overlooked. Thus Salfeld (1909) gives the *F. cycadea* reference as 1828, but this is a mistake. Brongniart cites Berger's reference and makes it quite plain that he took the specific name from Berger. It is not likely that Goeppert added to this confusion by changing the specific name to *Bergeri* because everyone seems to have known that it was a later substitution. The name *Bergeri* has been dropped for many years.

The generic name *Ctenopteris* was first used for this fossil by Saporta in 1873. He took the name from a manuscript of Brongniart and published it as Brongniart's genus, though Saporta would seem to be the responsible author. The question who is the author of *Ctenopteris* is, however, immaterial because the name is not valid, being an homonym, *Ctenopteris* having been used by Blume in 1828 as a genus of Recent ferns (allied to *Grammitis*). I am indebted to Dr. R. E. Holttum for pointing this out.

Nathorst (1886) instituted the new name *Ctenozamites* to replace *Ctenopteris*, not on the grounds that it was a homonym, of which he was unaware, but because he considered it unsuitable. He was convinced that the plant was no fern but some kind of Cycad and allied to *Ptilozamites*. Few authors accepted this but continued to use *Ctenopteris* on the grounds of priority, or because they thought it a fern. However, Schenk (1887) used the combination *Ctenozamites cycadea*. Nathorst gave no diagnosis nor adequate description but he made it clear that the name was to be used for *Odontopteris bergeri* (which he recognized as the same as *Ctenopteris cycadea*) and for *C. leckenbyi* from the Oolite of Yorkshire.

4. *Morphology*. The main new fact contributed here is that the rachis forks. Although the specimen has been damaged by the cliff fall or when collected, the continuity of the two branches is fortunately still visible.

This forking might have been recognized long ago because one of the specimens figured by Schenk (1887, pl. 3, fig. 13) shows forking, though at a point much nearer the leaf apex. Possibly forking is variable, or, as in *Ptilozamites nilssoni*, some leaves may fork twice.

5. *Anatomy*. The new facts here contributed about the anatomy of the lamina and rachis do give some help for comparison, but not much. Their main value lies perhaps in that they prove that plants with structure preserved are to be found in limestone nodules near Lyme Regis, and the information we have should be sufficient to identify another and less compressed petiole when one is found. Search should be made.

Apart from its stoma the lamina is unspecialized. It lacks, for example, the strongly developed transfusion parenchyma of many Recent Cycadales and also their hypodermis, but these facts are not ones to which comparative anatomists give weight. The stoma is more useful ; it is haplocheilic as in most Gymnosperms and this distinguishes it sharply from all Bennettitales. The general arrangement of the subsidiary cells and the arched shape of the guard cells agrees closely with the Cycadales but less closely with Conifers or *Ginkgo* or such few Pteridosperms as we know. The dome of cuticle over the stomatal pit is a peculiar feature shared by a few fossils, *Ptilozamites* spp. and certain species of *Pseudoctenis* and not seen in any Recent Cycad though Cycads do not differ fundamentally. The rachis, as far as it is known, may be very like that of a Cycad. The subepidermal sclerotic tissue may be a similar mixture of thick-walled fibres and assimilatory cells but the thick-walled fibres of Cycads are at least in several genera, longer and less freely pitted. In having small vascular bundles with scalariform tracheids it agrees with Cycads. These features are by no means exclusive of Cycadales, for they occur, for example, in the petiole of *Medullosa*.

6. *Systematic position*. The four best known species of *Ctenozamites* make a compact group and it is reasonable to regard them as forming a natural genus and to discuss them together.

These four are :

Ctenozamites cycadea (Berger) Schenk.

Ctenozamites leckenbyi (Leckenby) Nathorst (see Harris, 1943).

Ctenozamites sarrani (Zeiller) nov. comb. for *Ctenopteris sarrani* Zeiller, 1903 : 53, pls. 6–8.

Ctenozamites wolfiana (Gothan) nov. comb. for *Ctenopteris wolfiana* Gothan, 1914 : 142, pl. 26, figs. 2, 2*a*, 5, pl. 37, figs. 5, 6. A dozen other species have been described but are either poorly known or probably belong to other genera and they are not considered here.

C. cycadea and its allies were at first regarded as species of *Odontopteris* or allied to that genus and some kind of fern, and later by Nathorst as Cycads allied to *Ptilozamites*. It is now generally regarded as a Gymnosperm and by different authors placed more or less close to the Cycadales. Nathorst was chiefly impressed by the leathery texture of *C. cycadea* and the close resemblance between a pinna fragment of *C. cycadea* and a piece of the rachis of *Ptilozamites nilssoni*. To these we can add the very close resemblance of their cuticles, particularly their stomata, and the fact that the main rachis in both forks. The only important difference is that the leaf is once pinnate in *Ptilozamites* but bipinnate in *Ctenozamites*. We have no evidence to show whether the rachis forks in the other three species of *Ctenozamites*, but in *Ptilozamites* we are almost certain that it is simple in some species. While the difference between a simply pinnate and a bipinnate leaf is so obvious that it makes a basis for generic grouping of fossil leaves that is too useful to neglect, one may suspect that the plants could all have belonged to one natural genus.

We know nothing about the reproductive organs or other parts of the plant bearing *Ctenozamites* leaves, but we have probably the pollen producing organs of *Ptilozamites nilssoni*. These were described by Harris (1932) under the incorrect determination " *Hydropteridangium* " or *Hydropterangium marsilioides* Halle and renamed *Harrisia marsilioides* by Lundblad (1950) and then as *Harrisothecium marsilioides* by Lundblad (1961). It was attributed to *P. nilssoni* on the evidence of association and agreement in stomatal structure. This fructification is like a loosely organized cone, but its morphology is obscure. The main axis branches in all planes, the branches themselves branch and end in 2-valved capsules. Each valve contains a row of elongated microsporangia with pollen grains, each with two nearly opposite air sacs. If we may accept that *Harrisothecium* belongs to *Ptilozamites* its value in classification is negative in that it provides evidence against including the plant in the Cycadales and indeed in any other established group. The capsules look like those of *Williamsonia* or *Cycadeoidea* but they differ completely in pollen, and stomata, and in the mode of branching.

Ctenozamites (" *Ctenopteris* ") has been classified as possibly Cycadalean, possibly a Pteridosperm, a Cycadophyte or just a Gymnosperm *incertae sedis*. There is very little reason for preferring one to another, except that if the fructification is like *Harrisothecium* the Cycadales would be excluded and so would the Pteridosperms unless we extend the meaning of that extensive class still further. Whether it is a " Cycadophyte " is a matter of definition. The term is for many no more than a convenient abbreviation for the phrase " A Mesozoic Gymnosperm with a pinnately constructed leaf and *any* sort of reproductive organ ". It includes Cycadales and Bennettitales with totally different reproductive organs and stomata. If " Cycadophyte " is used in this way, *Ctenozamites* would be placed there readily enough. For other authors " Cycadophyte " is supposed to be some kind of large family of plants with a relationship that is real even if rather obscure. This is near to its original meaning and if such meaning is held, *Ctenozamites* should be left *incertae sedis*, and indeed the term Cycadophyte should be abandoned.

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PLATE 31

Ctenozamites cycadea (Berger)

Upper part of the specimen. Counterpart of what is shown in Text-fig. 1, A. × 1. V.36330.

PLATE 32

Ctenozamites cycadea (Berger)

FIG. 1. The rachis dichotomy. × 1.
FIG. 2. The lower part of the rachis showing stumps of two pinnae. × 1.

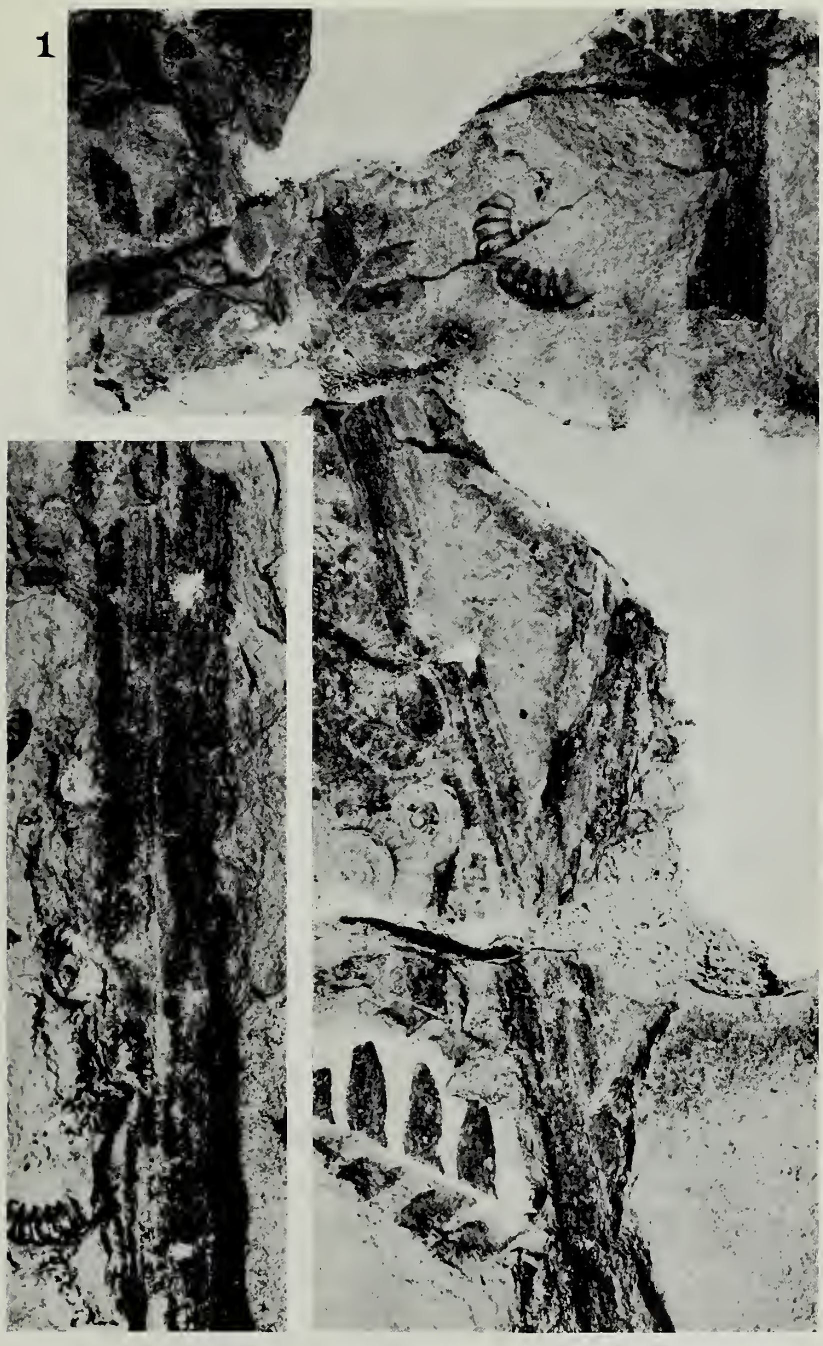
PLATE 32

Ctenozamites cycadea (Berger)

FIG. 1. The rachis dichotomy. × 1.
FIG. 2. The lower part of the rachis showing stumps of two pinnae. × 1.

1

2



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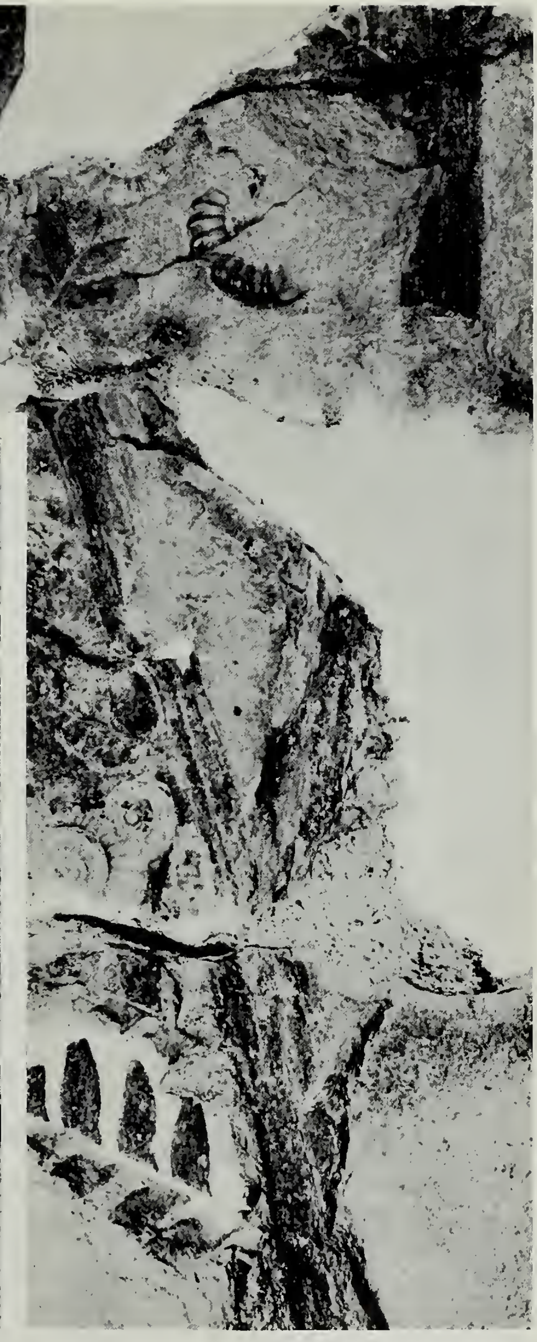

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